Variation in seed production and germination in 22 rare and threatened Western Australian *Verticordia* (Myrtaceae)

A Cochrane[1], K Brown[2], S Cunneen[3] & A Kelly[4]

[1]Threatened Flora Seed Centre, Department of Conservation and Land Management, Locked Bag 104, Bentley Delivery Centre, Perth WA 6983
[2]Environmental Weeds Action Network, 108 Adelaide Terrace, East Perth WA 6000
[3]CSIRO Centre for Mediterranean Agricultural Research, Floreat WA 6014
[4]24 Carnarvon St, East Victoria Park WA 6100
email: annec@calm.wa.gov.au

Manuscript received August 2000, accepted March 2001

Abstract

This study investigates the reproductive potential of 22 rare and threatened Western Australian taxa in the genus *Verticordia* (Myrtaceae) over a 5-year period. Considerable inter- and intra-specific variation in both seed production and germinability was demonstrated for the majority of taxa. The seed to flower ratio, or "seed set", ranged from 0% to 68% with an overall mean of 21% in 82 accessions representing seed from 48 populations of the 22 taxa. Percentage germination ranged from 7% to 100% with an average of 49% for 68 accessions. The precariously low annual reproductive capacity of some of the more restricted and critically endangered taxa threatens their survival and unexpected disturbance events may result in population decline or even localised extinction. Mitigation measures such as the reintroduction of plant material into new sites and the enhancement of existing populations through additional plantings may be warranted for many of Western Australia's rare and threatened *Verticordia*.

Keywords: *Verticordia*, seed production, germination

Introduction

Verticordia (family Myrtaceae, sub-family Leptospermoideae) consists of woody perennials largely endemic to the South West Botanical Province of Western Australia. This genus occupies a prominent place in many shrub and heathland communities along with other myrtaceaous genera such as *Beaufortia, Calytrix, Agonis, Leptospermum, Melaleuca, Chamelaucium* and *Calothamnus*. There has been a considerable increase in our taxonomic understanding of the genus in the past decade, and a revision in 1991 identified 3 subgenera, 24 sections, 97 species, and 62 subspecies and varieties (George 1991). Material was later re-examined and 100 species and 43 infraspecific taxa were described for the genus (George & George 1994). Many taxa in the genus are considered of high conservation value. There were 76 taxa of *Verticordia* on the Western Australian Department of Conservation and Land Management's Declared Rare and Priority Flora List (Atkins 1998). Seventeen of these were declared rare (WA Government Gazette 1999), and five of these were ranked under IUCN criteria as Critically Endangered by CALM's Western Australian Threatened Species and Communities Unit (Anon 1998b). Many populations are at risk of local extinction in the near future due to a range of threatening processes. These include disease, weed invasion, salinity, small population sizes, habitat fragmentation and/or continued land clearing.

The genus possesses many species with great potential for ornamental horticulture (George 1990). The often prominently displayed feathery flowers are borne singly but appear as heads or spikes and are generally brightly coloured, ranging from yellow to red to purple. The flowers are long lasting, and can be picked for the cut flower market. Between 1996 and 1998 over 1 million flowering stems of 23 taxa of *Verticordia* were bush picked from private, crown lands and cultivated stands for the cut flower industry (L Rohl, CALM, unpublished data). Over-picking of flowers from the wild has been impacting on wild populations of a number of species (*e.g. V. eryocephala*) with detrimental effects (McEvoy & True 1995).

Although there have been a number of studies on pollen germination and tissue culture propagation in *Verticordia* (McComb *et al.* 1986; Tyagi *et al.* 1992), there has been limited research conducted on the reproductive biology of particular species in the genus. Seed appears to be of the dependent embryo type (small embryos relative to the endosperm) according to classification by Atwater & Vivrette (1987). Tyagi *et al.* (1991) reported that in *Verticordia* only a single seed is set despite ovule numbers of up to 13 in some taxa. Our experience has shown that on rare occasions 2 and 3 seed per flower may form in taxa with multiple ovules (A Cochrane, personal observations). Houston *et al.* (1993) report seed set (based on seed to flower ratio) for *V. nitens* averaging 27% with a range from 0.6% to 54% and 36% for *V. aurea*. Tyagi *et al.* (1991) also reported low seed set for a range of taxa in the genus.

Holm (1988) considered that pollinators for this genus were likely to be unspecialised insects, but postulated that *V. grandis* may be bird pollinated due to the flower structure. Houston *et al.* (1993) reported apparent pollinator mutualism in *V. nitens* and possibly in *V. aurea.* Profuse flowering in some species of *Verticordia* pointed towards intense competition for pollinators (Holm 1988), and given the great range of floral morphology, scent, colour and flowering times, it is possible that many pollinators will be found to be highly specific.

Verticordia have indehiscent fruits (nuts) that usually contain a single seed and are shed annually. They are never discharged but the entire flower dries and breaks off below the receptacle. It is thought that dormancy in some members of the Myrtaceae (for example in *Chamelaucium*, *Verticorida* and *Darwinia*) is controlled by the seed coat inside the fruit that breaks down in time due to weathering and soil disturbance (Beardsell *et al.* 1993a). *Verticordia* plants for the nursery industry have traditionally been propagated vegetatively due to inadequate knowledge of seed collection and germination techniques (Watkins & Shepherd 1984). Relatively few studies have been undertaken on seed germination in this genus, although Ashby (1961) reported some success with *V. picta*, *V. chrysantha* and *V. brownii.* Over the past 5 years considerable developments have been made in the techniques required for successful germination of a range of Western Australian species (see review by Bell *et al.* 1993; Cochrane & Kelly 1996). Smoke responsiveness has been demonstrated in the genus (Dixon *et al.* 1995) and after-ripening requirements can be overcome with the addition of the growth hormone gibberellic acid (Cochrane *et al.* unpublished observations).

Over the past 5 years, seeds of a large range of threatened taxa in the genus *Verticordia* have been collected for conservation in Western Australia's *ex situ* program. The aim of this program is to conserve the genetic diversity of threatened taxa under low moisture and low temperature conditions for long periods of time (> 50 years) until material is required for recovery purposes (Cochrane & Coates 1994).

This present study assessed the reproductive potential of a range of rare and threatened taxa in the genus *Verticordia* through an analysis of seed set and germination data collected over a 5 year period. These data are useful as a basis for recommendations for conservation and management of the populations. Sound knowledge of germination mechanisms will enable adequate monitoring of seed viability in storage and enhances the opportunity to provide whole plants for recovery.

Methods

All *Verticordia* seeds used in this study were collected from wild populations between January 1994 and December 1998. Site names have been abbreviated due to the confidentiality of locational information for conservation flora. Seed stocks are held *ex situ* at the Department of Conservation and Land Management's Threatened Flora Seed Centre, a seed-based genebank for the conservation of genetic material from rare and threatened taxa. Seeds were tested for germinability freshly collected and, in many cases, after moisture content reduction and storage at −20 °C for periods of up to 5 years.

Seed set was assessed by sectioning 3 replicate samples of 100 old flowers (fruits) through the hypanthium to establish the presence or absence of a healthy seed (swollen, moist, white embryo). Calculation of seed set by the cut test method was based on the proportion of seeds to old flowers rather than the seed to ovule ratio. Seed to flower ratio was considered to be a more useful indicator of reproductive potential than seed to ovule ratio as rarely did more than 1 ovule per flower set. "Seed set" was therefore defined as the number of intact and healthy seeds for a given number of flowers. Some predation of developing ovules was observed during cut tests, although the level of predation was not quantified.

Seed germination trials were conducted under laboratory conditions. Seed sample sizes were dependent on the number of old flowers (fruits) collected, as well as the number of seeds obtained by the cut test (seed set) and ranged from 5 to over 1000 seeds ($\bar{x}$ 61). To aid germination, seeds were completely excised from the old flowers with a scalpel under a dissecting microscope. Prior to seed coat removal, flowers were soaked in distilled water for a minimum of 2 hours to soften the seed coat. Seeds were germinated in 90 mm glass Petrie dishes on a 0.75% (w/v) agar solution in temperature and light controlled incubation cabinets, using a 12-hour photoperiod. Cabinets were set at a constant 15 °C. A 2% solution of Previcure fungicide was added to the agar solution to inhibit fungal growth. Seeds were not surface sterilised prior to incubation. Petrie dishes were checked twice weekly and germination was determined by radicle emergence.

Previous research (A Cochrane, unpublished data) has indicated that many species of *Verticordia* are smoke responsive, and the seeds of those species requiring aqueous smoke treatment for optimum germination were soaked for 24 hours in a smoke solution obtained from Perth's Kings Park and Botanic Gardens and produced according to Dixon *et al.* (1995). After soaking, seeds were rinsed with distilled water prior to incubation. Growth promoters have been found to be necessary to cue germination in fresh seed of *Verticordia*, and the growth hormone gibberellic acid (GA_3) was added to the agar medium at either 25 mg L^{-1} or 10 mg L^{-1}.

Results

The number of ovules per flower in the genus *Verticordia* varies between species and ranges from 1 to 8 for the 22 taxa studied (Table 1). Rarely did more than 1 seed per flower reach maturity and as such the seed to ovule ratio ranged from 0.125 to 1 (Table 1). There was a broad range of inter- and intra-specific variation in seed set and germination within the genus (Table 2). The mean seed set for all collections was 21% (± 1.85) with a range from 0 to 68%. Population seed set was never greater than 68%, although seed set for a single individual within a taxon did reach 90% in *V. staminosa* subsp *cylindraceae* var *erecta* (see Fig 1). The mean percentage germination was 49% (± 2.96), range 7-100%, for 68 accessions.

Fourteen taxa are known to be obligate seeders; 4 are respouters, with 3 considered to have the potential to both resprout and seed. Information on the reproductive

Table 1

Fire response, number of ovules per flower, seed to ovule ratio, and percentage seed set and germination for 22 rare and threatened taxa in the genus *Verticordia*.

Species	Fire Response (Seeder/ Resprouter)	Ovules per flower	Seed/ ovule ratio	% seed set (± se, range)	% seed germination (± se, range)
Subgenus Chrysoma					
V. endlicheriana Schauer var *angustifolia* AS George (sect Chrysoma)	Both	2	0.5	11 (11)	24 (24)
V. staminosa ssp *cylindracea* AS George var *cylindracea* (sect Synandra)	Resprouter	2	0.5	58.0 ± 3.6 (53-65)	79.4 ± 11.6 (57-96)
V. staminosa ssp *cylindracea* AS George var *erecta* (sect Synandra)	Resprouter	2	0.5	33.5 ± 25.5 (8-59)	84.5 ± 3.5 (81-88)
V. staminosa C Gardner & AS George ssp *staminosa* (sect Synandra)	Resprouter	2	0.5	32.0 ± 6.1 (20-40)	76.7 ± 12.0 (60-100)
Subgenus Eperephes					
V. albida AS George (sect Pennuligera)	Seeder	7 or 8	0.125-0.14	43.8 ± 5.02 (20-68)	30.4 ± 8.6 (10-87)
V. comosa AS George (sect Pennuligera)	Seeder	8	0.14	17 (17)	47 (47)
V. attenuata AS George (sect Verticordella)	Seeder	6	0.17	22.8 ± 8.9 (8-48)	37.5 ± 5.9 (26-54)
V. bifimbriata AS George (sect Verticordella)	Seeder	6	0.17	33.5 ± 16.5 (17-50)	68 (68)
V. carinata Turcz (sect Verticordella)	Seeder	6	0.17	16.0 ± 2.1 (13-20)	34.7 ± 11.9 (11-48)
V. hughanii F Muell (sect Verticordella)	Both	8	0.143	15.0 ± 9 (6-24)	63.0 ± 6.0 (57-69)
V. spicata ssp *squamosa* F Muell (sect Verticordella)	Seeder	6 or 7	0.17-0.14	8.6 ± 2.1 (0-19)	43.0 ± 8.6 (7-86)
Subgenus Verticordia					
V. densiflora Lindley var *caespitosa* Turcz (sect Corymbiformis)	Seeder	1 or 2	1-0.5	25 (25)	73 (73)
V. densiflora Lindley var *pedunculata* AS George (sect Corymbiformis)	Seeder	1 or 2	1-0.5	25 (25)	78 (78)
V. dasystylis ssp *oestopoia* AS George (sect Penicillaris)	Unknown	2	1-0.5	6 (6)	75 (75)
V. fimbrilepis ssp *australis* Trucz (sect Verticordia)	Seeder	2	0.5	22.7 ± 4.5 (14-29)	56.7 ± 21.5 (15-87)
V. fimbrilepis ssp *fimbrilepis* Turcz (sect Verticordia)	Seeder	2	0.5	24.0 ± 2.5 (15-39)	53.8 ± 6.5 (25-86)
V. harveyi Benth (sect Verticordia)	Seeder	2	0.5	11.5 ± 3.1 (3-25)	33 (33)
V. helichrysantha F Muell Ex Benth (sect Verticordia)	Both	4 or 5	0.25-0.2	19.3 ± 8.4 (4-33)	47.3 ± 9.940 (29-63)
V. pityrhops AS George (sect Verticordia)	Seeder	2	0.5	5 (5)	-
V. plumosa var *ananeotes* (Desf) Druce (sect Verticordia)	Resprouter	4	0.25	5.4 ± 1.6 (2-11)	26.0 ± 7.0 (11-42)
V. plumosa var *pleiobotrya* (Desf) Druce (sect Verticordia)	Seeder	4	0.25	24 (24)	72 (72)
V. plumosa var *vassensis* (Desf) Druce (sect Verticordia)	Seeder	4	0.25	7.7 ± 2.6 (0-17)	46.0 ± 8.7 (25-75)

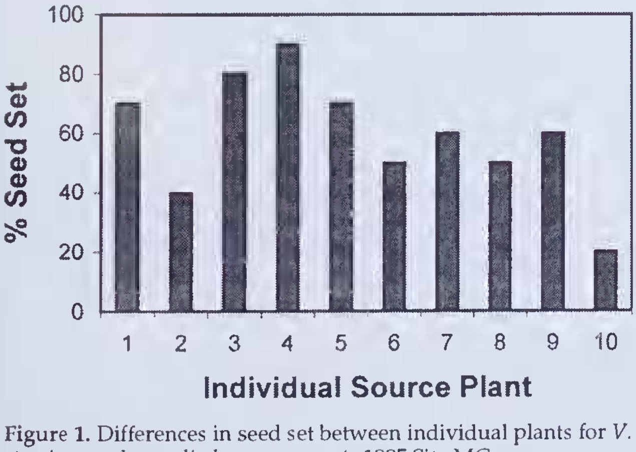

Figure 1. Differences in seed set between individual plants for *V. staminosa* subsp *cylindracea* var *erecta* 1995 Site MG.

strategy for one taxon (*V. dasystylis* subsp *oestopoia*) was not known.

Seed production and germinability for the 82 collections of *Verticordia* exhibited year to year (Fig 2A-C), population to population (Fig 3), plant to plant (Fig 4) and seasonal (Figs 5, 6) variation. The mean seed set and germination for each taxon was calculated (Table 1); however, the wide spatial and temporal variation make these figures somewhat misleading. Nonetheless these data provide a reference point to illustrate the variation between taxa. There were no apparent trends evident for seed set and germination or for reproductive strategy within the different subgenera or sections (Table 1). There was also no correlation between condition of the population as determined by location (road verge versus reserve or bushland) and health of population (degraded or healthy) and reproductive potential (Table 2). In addition, there was no correlation between intra-specific population size and levels of seed set (Table 2).

Discussion

Seed Production

It would appear from this study that rare and threatened taxa within the genus *Verticordia* exhibit excess flower production and a corresponding low seed to flower ratio, in keeping with previous results for common taxa in the genus (Tyagi *et al.* 1991; Houston *et al.* 1993). Lee & Bazzaz (1982) consider it more cost beneficial for plants to produce excess flowers and only allocate energy for seed production to those flowers with a minimal level of surviving embryos. Flower production is less energy draining than the necessary proteins and lipids required for seed production. Surplus flower production may enable plants to exploit favourable conditions such as increased resources or pollinator activity that occur unpredictably. Seasonal and yearly changes in seed set may be due to changes in flower density during the flowering period that may in turn affect pollinator assemblages, abundance and behaviour. It may also give a plant the opportunity to increase its

Table 2

Site location, condition (D=degraded H=healthy RV=road verge P=reserve, park, remnant bush), population size, time of collection, number of plants sampled, percentage seed set, and germination for 22 rare and threatened taxa in the genus *Verticordia*.

Species	Location	Condition	Population size	Time of collection	Plants sampled	% seed set	% germination	Seeds used in germination trials
V. albida	Site L	H RV	16	Jan-96	16	24	19	54
V. albida	Site L	H RV	16	Jan-97	12	20	30	53
V. albida	Site S	D RV	<20	Jan-96	5	50	87	8
V. albida	Site S	D RV	<20	Jan-97	7	56	12	50
V. albida	Site TSE	D RV	<50	Jan-96	10	42	27	15
V. albida	Site TSE	D RV	<50	Jan-97	20	38	10	50
V. albida	Site WW	H P	1000+	Jan-95	8	46	-	-
V. albida	Site WW	H P	1000+	Jan-96	500	68	29	78
V. albida	Site WW	H P	1000+	Jan-97	25	50	29	31
V. attenuata	Site BH	D RV	<100	Mar-94	30	13	36	47
V. attenuata	Site E	D RV	<50	Mar-94	20	22	34	35
V. attenuata	Site E	D RV	<50	Feb-95	30	48	26	66
V. attenuata	Site R	D RV	1000+	Mar-94	50	8	54	28
V. bifimbriata	Site D	H P	<30	Jan-95	12	50	-	-
V. bifimbriata	Site D	H P	<30	Feb-99	15	17	68	28
V. carinata	Site NIT	H P	1000+	Apr-96	100	20	48	23
V. carinata	Site NIT	H P	1000+	Apr-97	400	13	45	38
V. carinata	Site NIT	H P	1000+	Apr-98	100	15	11	36
V. comosa	Site NETS	H RV/P	100+	Jan-97	30	17	47	19
V. dasystylis ssp *oestopoia*	Site BC	D RV	8	Nov-97	8	6	75	16
V. densiflora var *caespitosa*	Site FNR	H P	100+	Feb-99	20	25	73	22
V. densiflora var *pedunculata*	Site WLH	D RV	<50	Feb-99	20	25	78	18
V. endlicheriana var *angustifolia*	Site MB	H P	1000+	Feb-95	50	11	24	17
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Jan-95	200	14	15	13
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Feb-96	200	29	87	45
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Feb-97	100	25	68	63
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Mar-97	25	15	30	40
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Feb-98	15	20	25	48
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Jan-96, Feb-96	8	39	79	168
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Mar-97	40	17	62	29
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Jan-98	30	20	32	54
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Jan-96, Feb-96	30	31	56	168
V. fimbrilepis ssp *fimbrilepis*	Site J7	D RV	100+	Mar-97	50	32	73	81
V. fimbrilepis ssp *fimbrilepis*	Site J7	D RV	100+	Jan-96, Feb-96	150	28	86	99
V. fimbrilepis ssp *fimbrilepis*	Site JNR	H P	300+	Feb-98	250	15	82	71
V. fimbrilepis ssp *fimbrilepis*	Site NH	D RV	13	Jan-96	10	20	46	63
V. fimbrilepis ssp *fimbrilepis*	Site R	D RV	10	Jan-98, Feb-98, Mar-98	10	19	30	23
V. fimbrilepis ssp *fimbrilepis*	Site TR	H P	100	Jan-99	100	37	44	1470
V. harveyi	Site BP	H P	1000+	Apr-94	16	13	-	-
V. harveyi	Site BP	H P	1000+	Apr-96	30	10	-	-
V. harveyi	Site BP	H P	1000+	Apr-97	50	11	-	-
V. harveyi	Site EPT	H P	1000+	Apr-95	200	7	-	-
V. harveyi	Site EPT	H P	1000+	Apr-97	50	3	33	9
V. harveyi	Site SET	H P	1000+	Apr-96	500	25	12	25
V. helichrysantha	Site CR	H P	1000+	Nov-94	200	33	63	104
V. helichrysantha	Site CR	H P	1000+	Oct-95	1000	21	50	54
V. helichrysantha	Site TB	H P	1000+	Nov-98	50	4	29	14
V. hughanii	Site A	H P	1000+	Mar-99	60	24	69	58
V. hughanii	Site HNR	D P	<30	Mar-99	8	6	57	21
V. pityrhops	Site EMB	H P	500+	May-99	200	5	-	-
V. plumosa var *ananeotes*	Site ANR	H P	<100	Mar-94	10	11	11	9
V. plumosa var *ananeotes*	Site ANR	H P	<100	Mar-94	20	3	18	11
V. plumosa var *ananeotes*	Site ANR	H P	<100	Feb-95	30	5	-	-
V. plumosa var *ananeotes*	Site ANR	H P	100+	Feb-98	150	6	42	19
V. plumosa var *ananeotes*	Site ANR	H P	100+	Feb-99	30	2	33	24
V. plumosa var *pleiobotrya*	Site M	D RV	500+	Feb-95	27	24	72	64
V. plumosa var *vassensis*	Site APV	D RV	50+	Feb-97	40	5	53	15

Table 2 (continued)

Species	Location	Condition	Population size	Time of collection	Plants sampled	% seed set	% germination	Seeds used in germination trials
V. plumosa var *vassensis*	Site APV	D RV	50+	Jan-98	30	9	44	27
V. plumosa var *vassensis*	Site E	D RV	<20	Feb-99	10	0	-	-
V. plumosa var *vassensis*	Site FR	H P	1000++	Feb-98	1000	0	-	-
V. plumosa var *vassensis*	Site FR	H P	1000++	Feb-99	90	7	75	8
V. plumosa var *vassensis*	Site GBR	H RV	100+	Feb-98	20	17	48	44
V. plumosa var *vassensis*	Site WLH	D RV	50+	Feb-99	17	16	33	82
V. spicata ssp *squamosa*	Site C	H P	11	Jan-96	5	18	52	46
V. spicata ssp *squamosa*	Site C	H P	11	Jan-97	10	7	29	21
V. spicata ssp *squamosa*	Site C	H P	11	Feb-98	11	19	24	54
V. spicata ssp *squamosa*	Site CR	D RV	1	Jan-97	1	4	60	5
V. spicata ssp *squamosa*	Site CYM	D RV	1	Jan-96	1	0.35	-	-
V. spicata ssp *squamosa*	Site CYM2	D RV	1	Jan-97	1	0	-	-
V. spicata ssp *squamosa*	Site NETS	D RV	1	Jan-97	1	1	-	-
V. spicata ssp *squamosa*	Site S	D RV	2	Jan-96	2	8	36	22
V. spicata ssp *squamosa*	Site S	D RV	1	Jan-97	1	14	50	6
V. spicata ssp *squamosa*	Site TSM	D RV/P	15	Jan-96	15	11	86	7
V. spicata ssp *squamosa*	Site TSM	D RV/P	15	Jan-97	13	12	7	31
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site PG	H P	30	Dec-95	7	53	57	14
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site PR	H P	200	Dec-98	33	65	96	100
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site VR	H P	50	Dec-98	12	56	85	103
V. staminosa ssp *cylindraceae* var *erecta*	Site MG	H P	200+	Dec-95	10	59	88	40
V. staminosa ssp *cylindraceae* var *erecta*	Site MG	H P	200+	Dec-98	50	8	81	21
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-95, Nov-95	20	36	60	45
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-97	30	40	70	50
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-96, Oct-96, Nov-96	50	20	100	24

offspring vigour through selective abortion. Surplus flower production may also provide an ovary reserve in case of mortality of flowers, or may provide a buffer during adverse weather conditions or during competition that may reduce pollen flow (Lee & Bazzaz 1982). The interacting factors of pollination failure, resource deficiency, predation and genetic defects causing developmental failure may cause pre-dispersal seed and ovule mortality (Fenner 1985; Wallace & O'Dowd 1989). A range of biological constraints can also lead to reductions in seed production (Owens 1995). These include (1) periodic or inadequate floral initiation, (2) asynchronous development and flowering, (3) floral abortion, (4) ovule abortion, (5) embryo abortion, and (6) failure of seeds and fruits to mature and our inability to determine maturity. Constraints and their importance will vary among species, sites and years and occur throughout all stages of development. Stephenson (1981) reports that whole fruit abortion is common among outcrossing perennials and that a low fruit to flower ratio (i.e. seed set) is observed in many species. Similarly, Wiens *et al.* (1987) noted that reproductive success as measured by seed to ovule ratio in outcrossing plants was considerably lower (22%) than in inbreeding plants (90%).

A number of researchers have reported that self-incompatibility in the family Myrtaceae contributed to low seed set (*e.g.* Briggs 1962, 1964; Prakash 1969; Rye 1980; Barlow & Forrestor 1984; Griffin *et al.* 1987; Beardsell *et al.* 1993b, Sedgley & Granger 1996). Despite widespread self-incompatibility within the family, recent research into the mating system of the rare *Verticordia fimbrilepis* subsp *fimbrilepis* has established that inbreeding rates are very high (J Samson, CALM, personal communication). Rye (1980) and Tyagi *et al.* (1991) also noted self-compatibility in a number of species in the genus. Tyagi *et al.* (1991) considered that low seed set in field populations of some species of *Verticordia* was determined by factors such as efficiency of pollen transfer, genetic diversity within populations and physiological constraints rather than loss of pollen fertility. They were unable to demonstrate that seed produced by inbreeding was viable, although recent studies (J Samson, CALM, personal communication) have now shown that 78% of seeds of *V. fimbrilepis* subsp *fimbrilepis* produced as a result of self-fertilisation were viable. McEvoy (1995) also reported that seed viability was not reduced by selfing in the common *V. eriocephala*. These data suggest that inbreeding depression is unlikely to be a cause of low seed set in this genus.

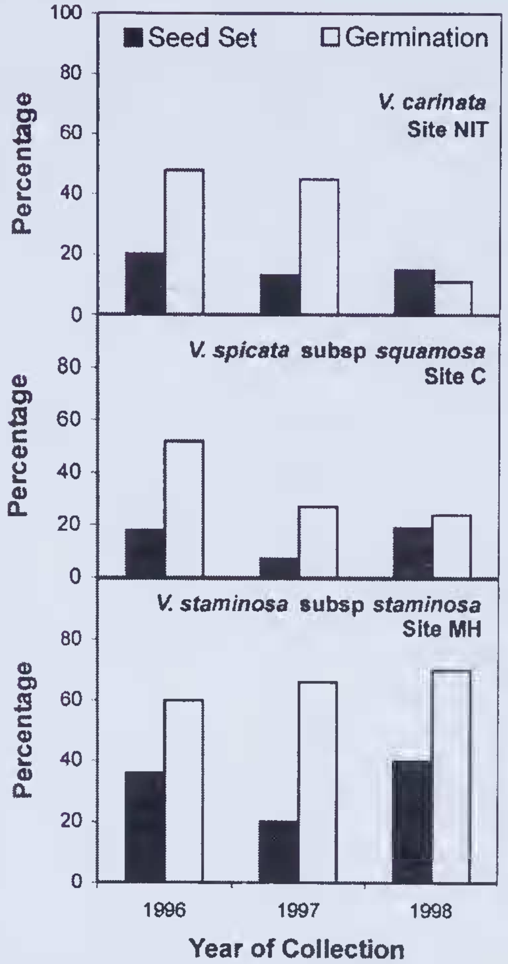

Figure 2. Difference in seed set and germination between years for *V. carinata* Site NIT, *V. spicata* subsp *squamosa* Site C, and *V. staminosa* subsp *staminosa* Site MH.

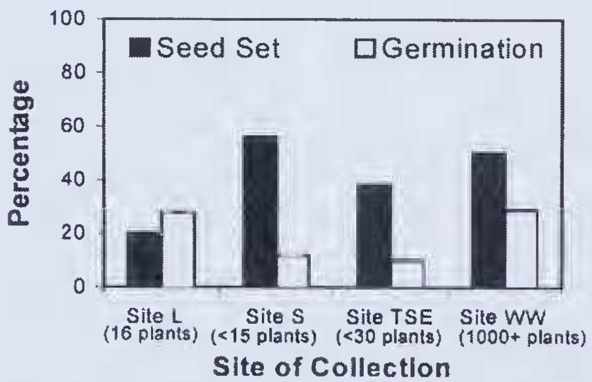

Figure 3. Differences in seed set and germination between sites of collection for *V albida* 1997 collections.

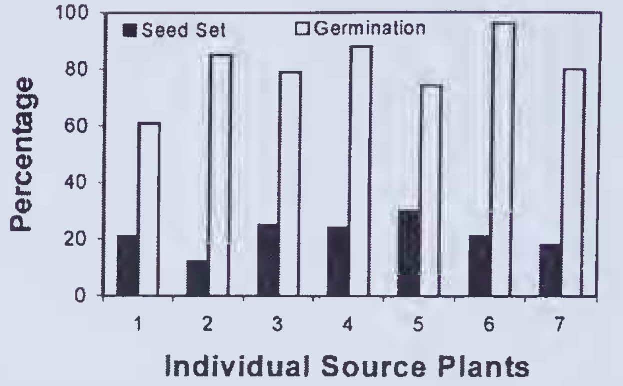

Figure 4. Differences in seed set and germination between individual plants for *V fimbrilepis* subsp *fimbrilepis* Site A, 1998.

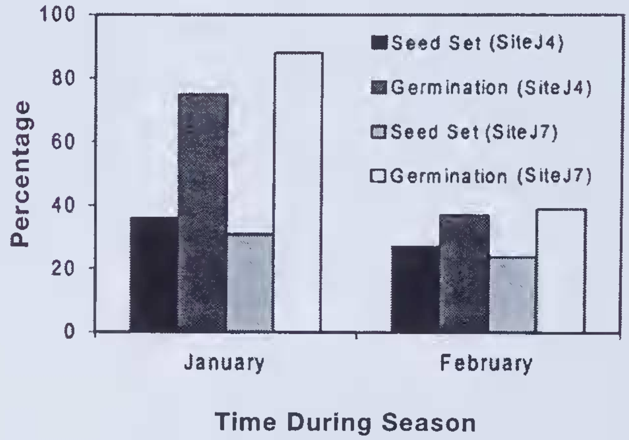

Figure 5. Seasonal differences in seed set and germination for *V fimbrilepis* subsp *fimbrilepis* 1996 collections.

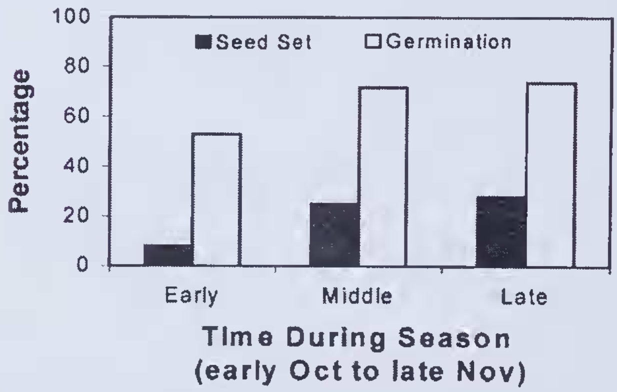

Figure 6. Seasonal differences in seed set and germination for *V staminosa* subsp *staminosa* Site MH 1996 collections.

Environmental stress and demographic structure of the population have also been known to contribute to low seed production (Jordano 1992) and can account for some of the wide variation in seed set noted between individuals, populations and years. However, this study demonstrated that smaller populations of *Verticordia* located on degraded road verges did not necessarily exhibit lower seed set than larger populations occurring in remnant bush or in reserves or bushland (Table 2). There appeared to be no difference in seed set between healthy and degraded sites indicating that environmental stress at a gross level may not be impacting on the reproductive capacity of those taxa studied. It is possible that reproductive success may be a function of plant maturity, although at the time of this study the age structure of each population was unknown. Another significant factor affecting seed set is the presence and health of pollinators, which may in part be related to the health of the site and opportunities for supporting pollinators.

Various studies have reported a relationship between seed set and life history (Wiens 1984; Ehrlen 1991;

Richmond & Chinnock 1994; Meney *et al.* 1997). It appears that reproductive success in some genera may in part be determined by the internal allocation of resources as dictated by the plants' regenerative mode (Carpenter & Recher 1979; Hansen *et al.* 1991; Ladd & Wooller 1997; Meney *et al.* 1997). In this study, there was no evidence to suggest that seed set in *Verticordia* varied between obligate seeding and resprouting species. The wide intra-specific variation in seed set makes it difficult to determine relationship between levels of seed set and regenerative mode and further investigations are required.

Seed Germination

The breakdown of seed dormancy in *Verticordia* appears to require not only the removal of the seed coat, which acts as a barrier to water uptake, but also the addition of growth hormones to overcome an after-ripening requirement. It is possible that the hypanthium and perianth might help protect the seed from weathering, thus maintaining dormancy. This has been observed in *Thrytomene calycina* (Beardsell *et al.* 1993c). Recent work on other genera in the family Myrtaceae (*Darwinia* and *Chamelaucium*) has also established the need for hypanthium removal and the application of growth hormones to aid germination (A Cochrane, unpublished data). Despite considerable inroads into understanding the germination requirements of the genus *Verticordia*, we are not achieving maximum germination in most cases from what appears to be healthy, mature seed. It is obvious that there is still a great deal more to be understood about the germination requirements of particular taxa. Further research is required to determine whether this incomplete germination is due to after-ripening requirements, to maturity of seed, to inadequate dormancy breaking treatments and/or to genetically related defects.

Given that sampling of material for *ex situ* conservation occurs on a random basis to enable the range of genetic characters and reproductive potential to be represented, it is not unexpected to find such intra- and inter-specific variability in germination. Germinability of seed will be affected by the environmental conditions under which the seed developed. It will also be affected by the timing of collection (see Figs 5, 6) and post-harvest conditions prior to germination. Germination differences among individuals have important fitness consequences and germination differences between populations could well be reflecting inbreeding depression (Menges 1991). There have been suggestions that there is a relationship between population size and germinability in species, with larger populations exhibiting higher germination than smaller populations (Menges 1991). Our data on *Verticordia* indicate no such relationship (Figure 3).

This study has demonstrated considerable variation in seed set and germinability in a range of taxa in the genus *Verticordia*. The precariously low annual reproductive success of some of the taxa studied indicates a need for considerable monitoring of the health and biology of these taxa over the long-term. Continued disturbance such as clearing, disease or fire may result in population decline or even localised extinction of some of the more critically endangered taxa. Changes in population size, degree of isolation and fitness are warning signs that populations may be vulnerable (Ellstrand & Elam 1993) and should cause concern to conservation managers. Regeneration plays a major role in the composition and floral diversity of plant communities. The regeneration potential of a population depends on the proportions of germinable seed successfully growing, maturing and attaining reproductive status, as well as the reproductive potential determined by seed set and germination. For most taxa the effective size of the soil seedbank remains unknown. Seedling survival through summer months is also unknown. Further stresses due to post-dispersal factors (seed predation and seedling mortality) in species that already exhibit low pre-dispersal reproductive success will critically restrict the ability of the taxon to reconstitute populations from seed, or to maintain levels of plants in the face of disturbance and senescence.

Seed set in plants occurring in intact vegetation is no greater than in plants located in degraded sites, but the ability of populations to attract and support pollinators may be dependent on the condition of the site and its associated vegetation. Despite the ability of plants to self-pollinate, the impact of reducing population size and health on the survival of plants and their reproductive capacity is unknown. Mitigation measures such as the reintroduction of material into new sites and the enhancement of existing populations may be warranted for many of Western Australia's rare and threatened *Verticordia*. The observed year to year and site to site variations in seed set and germination suggest a cycle of alternating high and low reproductive activity which may be affected by seasonal influences on fruit survival and maturation. Reproductive success in terms of seed to flower ratio may be a function of size, age, condition and genetic make-up of the plants, as well as seasonal factors and pollinator activity. Research into spatial and temporal factors (*e.g.* climatic data, nutrient status of sites, pollinator visitors, pollen loads, age structure and genetic variability within each population) affecting seed production and germinability in *Verticordia* is considered necessary to ensure local extinction of small isolated populations does not occur.

Acknowledgments: The authors wish to acknowledge the assistance of E George for identification of specimens and for the provision of information on ovule numbers and regenerative mode for the taxa utilised in this present study. Between 1992 and 1998 the Threatened Flora Seed Centre was funded by the Threatened Species and Communities Section, Biodiversity Group, Environment Australia.

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